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Kooijman, S.A.L.M.

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The role of bivalves in the Balgzand: First steps on an integrated modelling approach

S. Saraiva [a,*], L. Fernandes [b], J. van der Meer [c,d], R. Neves [e], S.A.L.M. Kooijman [d]

[a] Swedish Meteorological and Hydrological Institute (SMHI), Folkborgsvgen 17, SE-601 76 Norrköping, Sweden
[b] Action Modulers, Estrada Principal, 29 r/c Paz, 2640-583 Mafra, Portugal
[c] Royal Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands
[d] Vrije Universiteit, Dept. of Theoretical Biology, de Boelelaan 1087, 1081 HV Amsterdam, The Netherlands
[e] Instituto Superior Técnico, Environment and Energy Section, Av. Rovisco Pais, 1, 1049-001 Lisboa, Portugal

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ABSTRACT

The present paper describes a process oriented modelling tool that integrates physical, biogeochemical, ecological and physiological factors governing bivalve populated marine ecosystems. This modelling tool is the result of the coupling between an individual-based population model for bivalves (based on the Dynamic Energy Budgets theory, DEB) and a hydrodynamic/biogeochemical model (MOHID Water Modelling System). The model was implemented in the Balgzand area (Wadden Sea, The Netherlands) in a fine resolution domain to study mussel population dynamics and to quantify the influence of mussel communities on the pelagic system. Model results for a reference scenario (2009/2010) are in agreement with observations, and provide a consistent quantitative description of local hydrodynamics and biogeochemical cycles. The Balgzand acts as a sink of phytoplankton due to bivalves' filtration, and a source of ammonia, exporting about 40% more than the input flux. These results suggest significant ammonia regeneration. Results show that despite the long and almost continuous spawning season, only a few cohorts are able to survive. Early stage mortality (top-down), in particular cannibalism and shrimp predation, can control the persistence of new cohorts in the first month although starvation (bottom-up) represents the main cause of biomass loss in an overall. The tendency is that new mussel beds are formed in areas adjacent to already existing mussel beds and channel edges. Bivalves' activity intensifies the seasonal patterns of food and nutrients in areas close to the mussel beds, though not changing their overall spatial distribution. This study not only confirms but also quantifies mussels' potential to influence ecosystem functioning due to their role in nutrient cycling. As the first integrated modelling study that focus on the mussels' beds in the Balgzand, the main difficulties on the model design, setup and results analysis were overcome. The model can now be used further, tested and improved in the same or other systems in order to serve as an effective and reliable scientific and management tool.

1. Introduction

Bivalves, which are common to many coastal habitats, are probably ecologically and economically the best studied benthic suspension feeding group (Dame et al., 2001). The ability to predict the dynamics of bivalve populations in response to environmental change, natural or human induced, is useful for the management of coastal ecosystems, either with the purpose of commercial exploitation optimization, environmental impact assessment, climate changes implications or assessing the impact of exotic species introduction. Mathematical models have been used to address some of these questions. Although they can vary enormously in terms of complexity, their focus is either more oriented on (i) the eco-physiology of the individual bivalves, coupled or not with biogeochemical and biological models, but with 'simplified' descriptions of physical processes (e.g. Brinkman et al., 1993; Baretta et al., 1995; Dowd, 1997; Scholten and Smaal, 1998; Ren and Ross, 2001; Savina and Ménesguen, 2008; Brigolin et al., 2009; Ferreira et al., 2009) or on (ii) physical transport, using complex physical models where only 'simple' formulations for biogeochemical/biological processes were introduced, e.g. GETM (Burchard and Bolding, 2002), COHERENS (Luyten et al., 1999), MOHID Water Modelling System (Miller and Pinder, 2004). Generally, the first group of models aims to predict the bivalve production and the sec-

* Corresponding author.
E-mail address: sofia.saraiva@smhi.se (S. Saraiva).

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ond group aims to predict the impact of bivalves activity on system properties, such as primary production. The constant developments in computer hardware and programming languages enabled the development of models that couple complex descriptions of both ecological and physical processes. The challenge is now to get better predictions of bivalve production and population dynamics in interaction with an ever changing environment by improving the description of food availability and relevant physical processes, supplied by the 'physical transport' type of models. Some examples of this approach can be found in the literature (e.g. Klinck et al., 2002; Hofmann et al., 2006; Goff et al., 2017)

Several difficulties arise compared with the traditional modelling approach followed for phytoplankton and zooplankton. Most of these difficulties are caused by two facts: (i) bivalves have both a pelagic stage, where they are transported in the water column and directly depend on physical processes, and a benthic stage (e.g. de Vooys, 1999); (ii) their food requirement (bottom-up processes) and their interactions with other species (competition and top-down processes) strongly change throughout their life cycle (embryo, juvenile and adult stages). Reproduction and recruitment success can not be deterministically predicted if these two facts are not properly addressed. In some of the current modelling approaches the problem is solved either by imposing spawning events at a specific time (e.g. Maar et al., 2010) or by considering them dependent on environmental variables (e.g. Gerla et al., 2014). Some studies also focus on the dispersal and settlement of the larvae (e.g. Bidegain et al., 2013). However, in those studies the reproduction is detached from the bivalve development stage. In addition, understanding top-down control requires the simulation of the individual size, throughout their main live stages (larvae, juvenile and adult), since predators have size preferences. Size structure in the population has been normally neglected or imposed, though. Probably because most models have been developed for environmental impact assessment, where either the size structure is artificially controlled, as in aquaculture systems, or simply because it is found too complex. However, model aims go now beyond aquaculture assessments and new questions are raised, for example on population responses to climate change. Other examples are related to the introduction of new species in lower, same and upper trophic levels, changes in food quality, changes in habitat morphology, changes in hydrodynamics, temperature or salinity. All these questions can only be addressed if size structure is considered in the population because the underlying processes are size depended and consequently their relative importance in time and space and that can be done through the simulation of the individual bivalve development. For this purpose, energy budget models have received some attention (Beadman and Kaiser, 2002), in particular the DEB theory, proposed by Kooijman (1986, 2000, 2010). It is based on a mechanistic view of an organism's metabolic processes, including growth, maturation and reproduction, where the basic principles and formulations are valid for all different stages of the individual. The direct consequence is that the same set of equations can be used to simulate the complete life cycle of a bivalve. This is an advantage in the coupling with hydrodynamic and biogeochemical models that already have a high level of complexity. Yet, this approach can significantly increase model complexity, i.e. higher number of state variables, more/different uncertainties to cope with, higher number of parameters to estimate, larger amount and variability of input data, higher computational time, and also larger volumes of output results to analyse.

Advantages and disadvantages of complex models use have been discussed in the last years (e.g. Fulton et al., 2003; Cury et al., 2008; Hannah et al., 2010), although with more focus on fisheries and end-to-end models. Conclusions are not yet established, but the fact is that very simplistic models fail to capture critical interactions and system components, but extremely complicated models can be impacted by uncertainty, computational cost and lack of accuracy (Fulton, 2010; Hannah et al., 2010). Models are suitably complex if all critical processes, drivers and components under scrutiny are captured (Fulton, 2010), which can be difficult to assess. In this paper, with the aim of predicting the bivalve population dynamics and quantify their influence on the pelagic system, we propose that the model should be able to simulate the size structure of the population, based on the individual development, through its main life stages (larvae, juvenile and adult) in a dynamic environment with changes in nutrients, temperature, and food driven by physical processes, as well as predators' seasonal abundance. Following this idea, the present paper describes a process oriented modelling tool that couples an individual-based population model for bivalves (based on the Dynamic Energy Budgets theory, DEB) and a hydrodynamic/biogeochemical model (MOHID Water Modelling System) and it implementation in the Balgzand area (Wadden Sea, The Netherlands).

2. Material and methods

2.1. Model description

2.1.1. MOHID Water Modelling System

MOHID (www.mohid.com) is a three dimensional (3D) water modelling system developed at Instituto Superior Técnico (IST), University of Lisbon. It consists of a set of coupled models that aim to simulate the main physical and biogeochemical processes in aquatic systems (Miller and Pinder, 2004). MOHID has been implemented and validated in different coastal/estuarine areas (e.g. Leitão et al., 2005; Trancoso et al., 2005; Saraiva et al., 2007; Vaz et al., 2009). The system is based on the finite volume concept and it is designed in a hierarchical modular structure, using an object oriented approach. The hydrodynamic model solves the primitive continuity and momentum equations for the surface elevation and 3D velocity field for incompressible flows, in orthogonal horizontal coordinates and generic vertical coordinates, assuming hydrostatic equilibrium and Boussinesq approximation (Martins et al., 2001). Momentum, mass and heat transport are computed using a generic 3D advection-diffusion library including high order advection schemes. It also includes a fine sediment transport module simulating settling, deposition and erosion for a generic class of particles and/or particulate matter. Erosion and deposition fluxes depend on bottom shear stresses that are calculated as function of near bottom currents and wave induced stress. The model comprises several modules to compute pelagic biogeochemical processes. The current study uses the Water Quality Module, based on formulations initially developed by the US Environmental Protection Agency (EPA) (Bowie et al., 1985). It is considered a NPZD model and its base features include: explicit simulation of nitrogen and phosphorous cycles; assumption of constant C:N:P ratios for organic matter and plankton; one group of phytoplankton, one group of zooplankton, dissolved nutrients and dissolved and particulate organic matter (detritus). The pelagic ecological processes parametrization is mainly adapted from EPA. Modelled benthic ecological processes, occurring in deposited sediments, include the mineralization of organic matter. Detailed information on the model structure, formulations and default parametrization can be found in www.mohid.com.

2.1.2. Individual based population model for bivalves

The population of bivalves is represented by several cohorts. Each cohort consists of a number of identical individuals born at the same time and with the same properties (e.g. size, biomass, state of development). The individual model is the standard DEB model (Kooijman, 2000, 2010), coupled with a feeding processes model,

specifically designed for bivalves (Saraiva et al., 2011). DEB theory assumes that the assimilated energy is first stored as reserve; subsequently the reserve is utilized to fuel the other metabolic processes, following the so-called κ-rule: a fixed fraction κ of mobilized reserve is used for somatic maintenance and growth, the rest is used for maturity maintenance and maturation (embryos and juveniles) or reproduction (adults). The allocation of energy to reproduction is temporarily accumulated in a reproduction buffer. A spawning event, which is dependent on temperature and gonad-somatic mass ratio (GSR), empties the reproduction buffer and gives origin to a new cohort in the system. Different types of particles, food and/or inorganic material, can be retained by bivalves through filtration. The model also assumes that the organism is able to use the reproduction buffer to cope with somatic maintenance costs (reabsorption of gametes) during starvation periods. During extreme starvation structure will be used, meaning that the organism's flesh shrinks, though maintaining the same shell length. In the same line, the bivalve is able to reduce its maturity level in order to cope with maturity maintenance (rejuvenation). To simulate possible differences between individuals (e.g. position and extreme local food depletion) within one cohort, an extra starvation mortality is considered when the condition of the individuals is low. This assumption pretends to simulate the death of individuals in the cohort due to local food depletion preventing the sudden death of the whole cohort. A schematic representation of the individual model and a list of the main parameters can be found in the supplementary material but a detailed description is presented in Saraiva et al. (2012) where the model performance was tested for different locations in the North Sea.

At the population level the model includes: initial egg mortality, background mortality, food competition, cannibalism, and imposed predation by shrimps, crabs and birds. Predator abundance and intake are considered a forcing function in the model, meaning that there is no feedback from the bivalve population on the predators. Each predator has a prey size range preference, and the predation impact in each cohort is proportional to the fraction of the number of individuals in the cohort and the total number of prey available. More detail on the population model formulations, assumptions and setup can be found in the supplementary material, and a full description in Saraiva et al. (2014). The coupling with the ecosystem model enabled the inclusion of two additional mortality effects on the population due to: (i) exposure to high velocities; and (ii) non suitable substrate for settlement. When exposed to high velocities mussels experience not only difficulties in feeding (Newell et al., 2001), but they can also be flushed away and eventually die. This study assumes that the death of mussels occurs when velocities are higher than 0.5 m/s (calibration parameter). Based on the fact that mussels have a preference to settle on substrates with coarse shell debris (wa Kangeri et al., 2014) the model assumes a settlement probability that is site dependent. Non-settled bivalves will eventually die, due to the effect of currents or burying. In addition, it is also assumed in the model that settlement occurs instantaneously when, and where, the individual length is higher than 0.026 cm (de Vooys, 1999).

2.1.3. Coupling biological and physical processes

The coupling philosophy assumes that the biogeochemical processes only depend on the environmental and physiological conditions of the individuals in a specific place and time. In MOHID, which is based on a computational grid to solve the transport equations, the methodology consists in building a biogeochemical module, organized in such form that the *sinks and sources* term is independent of the grid and of the grid cell location. This term is solved separately, but consistently, from the advection and diffusion terms. This independence allows the biogeochemical module to be implemented in any type of grid (1D, 2D, 3D) and can thus be seen as a zero-dimensional model, where external forcing conditions are provided (ex: light, temperature, salinity) and mass fluxes between state variables (e.g. phytoplankton, ammonia, bivalve) are computed for each control volume using only the *sinks and sources* term of the equations. This is also an efficient way to guarantee a high level of robustness in the code and to maintain it. The present study followed this methodology by building a Module Bivalve that computes the time evolution of bivalve properties (e.g. reserves, structure, length) for each cohort in each grid cell, as well as the correspondent effect on other water properties concentrations (e.g. phytoplankton, ammonia) due to their activity, illustrated by Fig. 1. MOHID structure also enables that almost any process can be switched on/off. As a result, the model is flexible and easy to use in different systems, conditions, scenarios and most of all, enables the study of particular processes within the system. The bivalves' state variables make use of this structure. For example, bivalve larvae transport can be switched on/off depending on the individual length. During the larvae phase the individual is subject to transport by currents and turbulence, and once it reaches a certain size (settlement size), the individuals settle, and the transport is switched off. In addition, the model configuration on this study assumes that food availability is determined by phytoplankton concentration and mussel larvae (cannibalism) and that total suspended matter can be filtered but not ingested by the individuals.

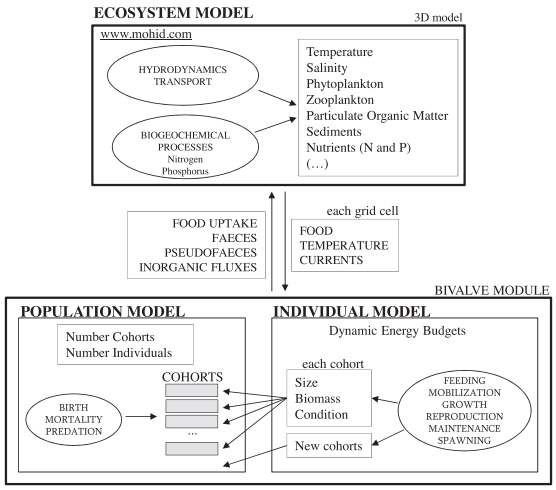

Fig. 1. Schematic representation of the coupling between the individual population model and the ecosystem model: model structure, links and information exchange in each time step.

2.2. Study area

The model is implemented for the Balgzand, an intertidal area approximately 50 km^2 in size, and located in the westernmost part of the Dutch Wadden Sea (Fig. 2). A long term sampling program at Balgzand started in 1970 and many studies have been performed in the area (and in the Wadden Sea) over a wide range of topics: physical processes, biogeochemical cycles in the water column and sediment, primary production, zooplankton, bivalves, shrimps, crabs, birds. The sum of all these studies constitutes an important source of knowledge on the system processes and dynamics. As a result, the Wadden Sea, and in particular the Balgzand, is suited to perform an integrated modelling study as proposed, as a high volume of information and data in several fields is required. Fig. 2 presents selected monitoring stations from different sources and projects. These locations correspond to field data stations with recent and consistent field data records that are further used to calibrate and validate the model. At the same time, their distri-

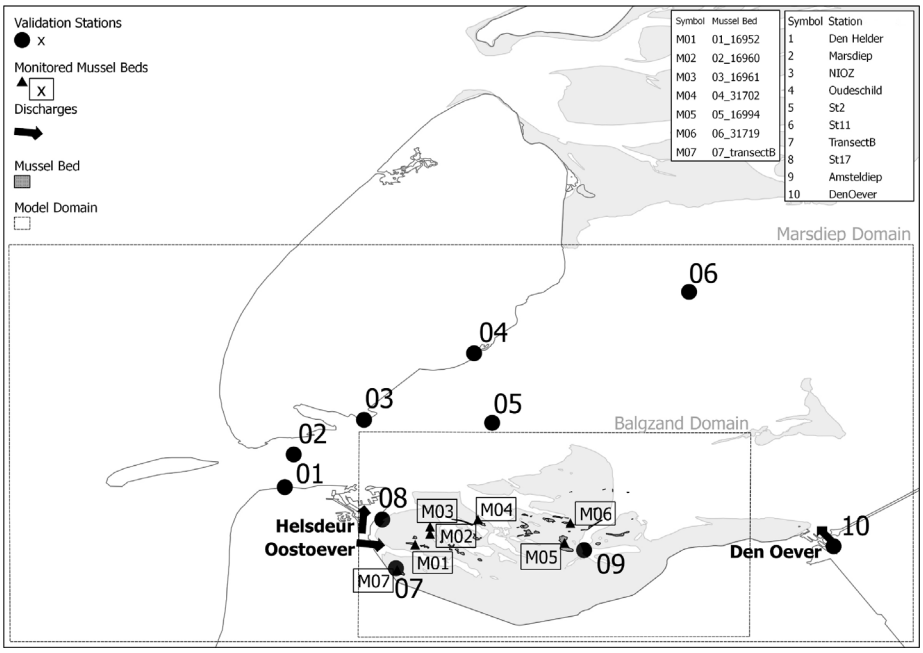

Fig. 2. Balzand area: mussel bed location, fresh water discharges and monitoring stations used for model validation.

bution provides an insight about the range of concentration and model performance in the different areas. Station 01 (Den Helder), 04 (Oudeschild) and 10 (Den Oever buiten), represent stations managed by Rijkswaterstaat with information on the water level. Station 02 (Marsdiep Noord), also from Rijkswaterstaat, has information on the concentration of some of the target water properties. At Station 03 (NIOZ Jetty), a continuous sea surface temperature and salinity observations that are being recorded for more than 30 years (van Aken, 2008a,b), as well as chlorophyll-a concentrations and total suspended matter, managed by Royal NIOZ (http://www.nioz.nl/colours). Stations 05, 06 and 08 are monitoring stations included in the IN PLACE project (NWO), carried out by the Royal NIOZ (Leote et al., 2016). Stations 07 and 09 correspond to stations where the model results will be shown in more detail. Stations M01 to M06 correspond to mussel beds included in a long monitoring program performed by IMARES within the WOT Fisheries program, commissioned by the Dutch Ministry of Economic Affairs (van den Ende et al., 2012). Finally, station M07 represents one mussel bed included in a long term monitoring program that provides information on the benthic fauna in the Balgzand, twice annually since 1970 (Beukema and Dekker, 2007).

2.3. Methodology

The reference scenario corresponds to a period from August 2008 until December 2010, when most of the data is available. The conditions imposed were, as much as possible, based on observations from this period reported in papers, reports and/or websites. When not possible, the model was forced with average conditions. Detailed description are given in the next sections. Initial values on the water column concentrations were obtained by a previous model run of two years. Results are analysed and compared with field data, in order to validate and test the model performance to describe the main processes. Next, the effect of the mussel beds in the system dynamics is quantified by a simulation without mussels. Results, with and without mussels, are compared in terms of temperature, salinity, total suspended matter, phytoplankton, ammonia, nitrate, inorganic phosphorus concentrations and bivalves' density time series in particular sites. Model results were also integrated over larger areas (integrated boxes) and fluxes across areas were computed by integrating the solution along the box boundary. Boxes were defined as follow: box 0 represents the Balgzand area in study; box 1 represents the area of influence from the Marsdiep channel; box 3 represents the area mostly influenced by the Den Oever discharge and the inside of the Wadden Sea; and box 2 represents a transport area, where water from the different sources is mixed.

2.4. Model setup

Morphologically, the Balgzand is a small but complex shallow area of the Wadden Sea with extensive tidal flats. A significant fraction of the total area, about 70%, is dry during low tide. Hydrodynamic circulation in this area is made through a series of small channels and it is mainly driven according to the local bathymetry, tide, wind and fresh water discharges. Tide and wind driven circulation is greatly influenced by processes occurring in the North Sea and the Wadden Sea. Although there are extensive amounts of data describing environmental conditions in these two systems, it is not always possible to provide boundary conditions for all model variables. Thus, in order to provide a higher quality estimation of boundary conditions, a general model was setup for the Marsdiep area in which a sub-model for the Balgzand area was nested (Fig. 2), The Marsdiep model uses a regular computational grid with 400 m resolution. The Balgzand model uses a nesting ratio of 1:4 (i.e. 100 m horizontal resolution). The high resolution in the Balgzand area is required in order to accurately simulate the narrow channels, estimate water flows and the drying and flooding of intertidal areas, particularly important when studying mussels dynamics. The bathymetry data was derived from the Vaklodingen data set published by Rijkswaterstaat (http://publicwiki.deltares.nl/display/OET/OpenEarth) and interpolated to the computational grids. In terms of vertical discretization, the model was setup in depth integrated model (2D). This option was made mainly due to computational restrictions and was deemed an acceptable approximation for the Balgzand area due to its shallowness. At the open boundary, the model is forced by the water elevations and current velocities derived from The Rijkswaterstaat Kuststrook-fijn model

(Philippart and Hendriks, 2005), a storm surge model for the North Sea, which results are provided by Deltares OpenDAP server. At the water surface, meteorological data from the De Kooy station was used to calculate momentum and heat fluxes. A statistical comparison with neighboring stations (Texelhors and Vlieland) showed minor variability in the measured parameters, particularly wind intensity and direction (results not shown). De Kooy time series data was thus selected based on the higher frequency of observations and less data gaps. Horizontal gradients in meteorological parameters were not considered. At the bottom, shear stresses were computed based on currents and waves (simulated by a limited area wind fetch based model), and used to estimate particulate matter fluxes due to deposition and erosion.

Several water discharges can be found in the study area but only three, presented in Fig. 2, are considered relevant: Helsdeur (next to the inlet), Den Oever (with a significant flow) and Oostoever (closer to the study area). Den Oever discharge is located in one extremity of the Afsluitdijk that closes the IJsselmeer, and for that reason the discharge properties are assumed to be equal to the conditions found in the lake. Data from several monitoring stations, managed by Rijkswaterstaat, is used to estimate the discharges properties. The necessary assumptions and considerations made to estimate the discharges and boundaries properties are summarized in the supplementary material. Because no specific information was found for Helsdeur and Oostoever discharges, the model assumes the same properties as considered for Den Oever discharge (except flow, temperature and salinity). Observations were used as much as possible, although data prior to 2000 was not considered because an important reduction of nutrients loads to the system has being detected in the last decade (Philippart et al., 2010). When possible, the seasonal variation of properties was considered, by using the data itself or by using a computed average seasonal pattern (by monthly or daily averaging the available values) for the periods without data. When this was not possible, a constant average value was used. Temperature and salinity at the Wadden Sea boundary were obtained by the interpolation of several time series results (vertically averaged) obtained from an implementation of the GETM model for the Wadden Sea, recently presented by Duran-Matute et al. (2014).

2.4.1. Mussel beds and predators

The initial mussel bed distribution in the model simulation was based on the mussel bed contours and densities (number of mussels per m^2), as estimated by IMARES 2008. Some of the mussel beds are monitored on a continuous basis (Fig. 2). For the mussels beds without further information, an average density value was assumed. The size distribution observed in mussel bed M07 was assumed for all other mussel beds, since no information was available. Initial conditions for the individual state variables (reserves, structure, maturity, reproduction buffer and age) were estimated from the results of a pre-run the DEB model, considering an average seasonal pattern of temperature and food conditions in the system. Predator abundance (supplementary material) is assumed to have seasonal variation in the system: shrimps abundance was adapted from Beukema (1992); crabs from Smallegange et al. (2009) and birds from Andreas Waser (unpublished data).

As an exercise, in order to quantify the effect of predation in the mussel spatial distribution, two additional short scenarios (April to January) were performed: (1) with predators (shrimps, crabs and birds) and (2) without predators. Both simulations used the same initial condition and the same set of parameters: the simulation starts with a constant spatial distribution of larvae with high concentration (1×10^6 individuals/m^2) and it assumes a settlement probability of 100%.

2.4.2. Settlement probability

The settlement probability map (supplementary material) is based on a qualitative index for the amount of shells in samples collected during 2013, in the Wadden Sea, in the SIBES-monitoring program, carried out by Royal NIOZ (Compton et al., 2013). The observations made at several stations were interpolated to the model domain and converted into settlement probability values by assuming that a large amount of shells and the mussel bed areas have 100% probability, no shells corresponds to a value of 10% and intermediate values follow a linear regression.

3. Results

3.1. Hydrodynamics

Hydrodynamic conditions (water elevations and depth integrated currents) were simulated for the period of August 2008 to the end of 2010. Model results were validated by comparing them with water elevations observations for several stations. Coefficients of determination (R^2), bias and root mean square errors asserted the ability of the model to reproduce the observed dynamics (supplementary material). Although no current velocities data were available for validation, the significant agreement between the water level predictions and observations, as well as temperature and salinity, is a solid indicator of the validity of the hydrodynamic part of the model.

From the hydrodynamic model results, one can derive quantities relevant for describing and understanding the Balgzand ecosystem dynamics, such as residual circulation, emersion times and residence time of water. The residual depth integrated flux (supplementary material) was computed by averaging the water fluxes divided by the grid cell width for each grid cell, and then divide the resulting value for the average water column height for each grid cell. Results show that residual circulation is mainly established along the main channels from east to west. There is low input of water entering directly from the North Sea through the Marsdiep, being this water recirculated along the Balgzand during ebb mixed with the Den Oever fresh water input. Emersion time is shown in percentage of time that each grid cell was emerged, during the year of 2009. The residence time of the water in the Balgzand area was determined following the methodology proposed by Braunschweig et al. (2003), using a lagrangian approach. The study revealed that the values can range from 3 to 16 days (Appendix A).

3.2. Biogeochemical properties

At all monitoring stations, strong seasonal patterns occur in the data and these patterns are generally well described by the model predictions (examples on Figs. 3–5). In general, temperature rises during spring and summer and starts to decrease in the beginning of autumn. Phytoplankton concentration shows a bloom in spring (and a smaller bloom in 2010 early autumn) with a consequent decrease in nutrient availability. In addition, the model predicts a daily oscillation that can be explained mainly by tide, although light limitation effects during the night on phytoplankton growth and nutrient uptake can contribute too. The model reproduces not only the dynamics but also the range of the observations, although some differences can be noticed. Salinity and total suspended matter (TSM) range is globally lower in the model, particularly at the stations 05, 06 and 08 where detailed observations were made at different depths during a complete tidal cycle. Those differences can be the result of sediment transport model limitations and related to the 2D setup. Nutrients concentrations are generally higher in the model, but the lower limit is within the range of the observations. Inorganic phosphorus concentration at station 08 (Fig. 5) is much

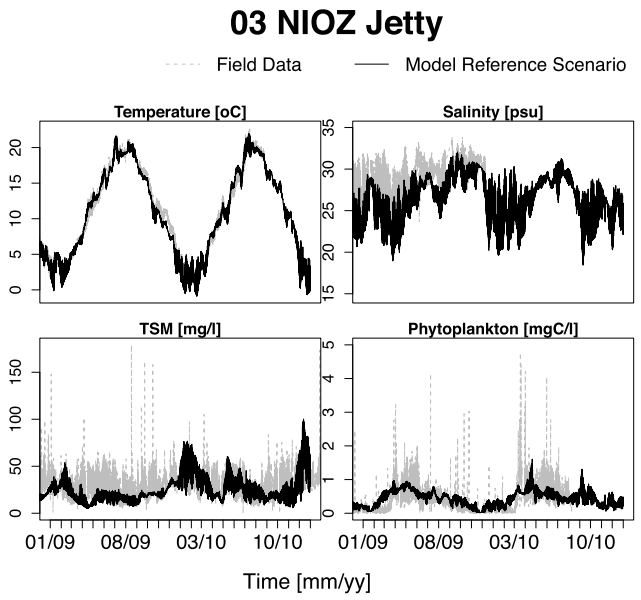

Fig. 3. Station 03, NIOZ jetty: model vs. observations.

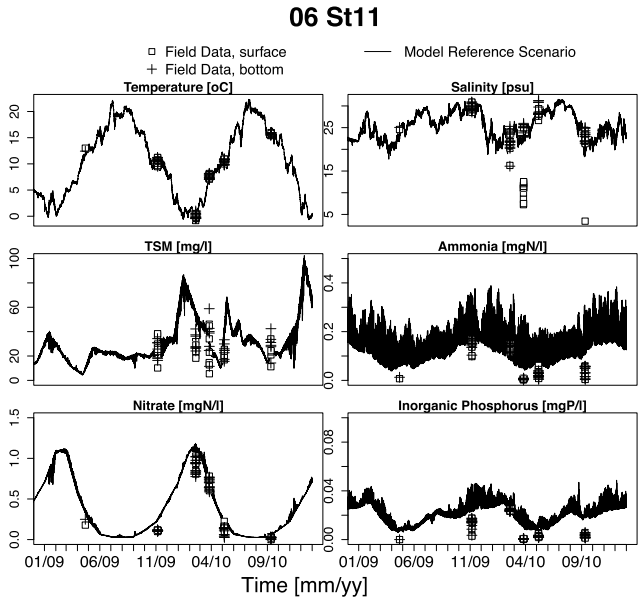

Fig. 4. Station 06: model vs. observations.

lower than the observations. The predicted values are in the same order of magnitude as the Oostoever discharge, though, indicating that at this location the effect of the discharge is significant and it is possible that the real discharge concentration is higher.

The spatial distribution of the target variables at high tide in spring and low tide in winter show that the Balgzand has particular conditions that neither directly reflect the conditions from the North Sea nor from the Wadden Sea. In spring, temperature, as well as phytoplankton and ammonia are higher in the Balgzand. In contrast, phosphorus distribution in spring shows lower values. Den Oever (IJsselmeer) discharge influence is clear, both in spring and winter. It has an important effect on the Balgzand, due to its high flow through one important channel that transports water to an extensive area, at least at normal hydrodynamics conditions. Although not possible to be detected in the presented figures, discharges from Oostoever and Helsdeur can also influence the surrounding area but only at the local scale.

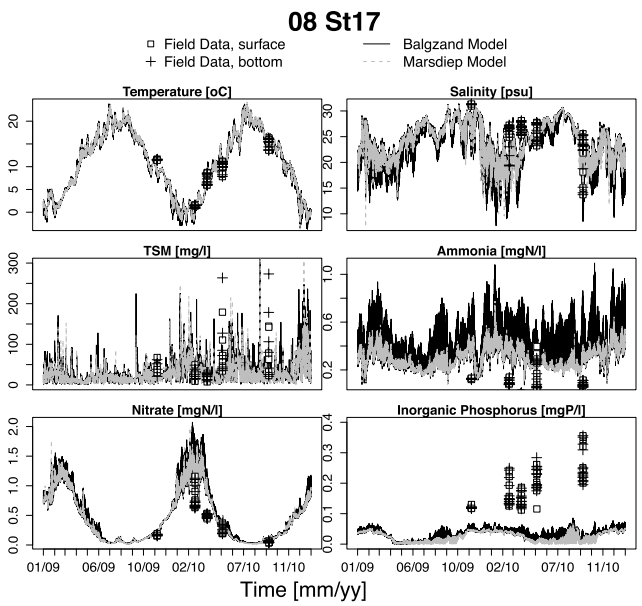

Fig. 5. Station 08: model vs. observations.

The mass fluxes analysis between the integrated boxes (Fig. 6) confirms that most nutrients and phytoplankton mass flux enter the Balgzand from box 3 (i.e. contribution from Den Oever discharge) and leaves the area to box 2. In an overall analysis of the average mass fluxes per year, the Balgzand acts as a sink of phytoplankton by consuming more phytoplankton than the input flux; and a source of ammonia, by exporting more than the input flux.

3.3. Mussel beds

Temperature and food availability (phytoplankton), in addition to physical conditions (emersion time and water depth), control mussel bed dynamics. Not surprisingly, mussel growth and development show spatial variability (Fig. 7). One year after the beginning of the simulation, cohort 1 no longer exist in some areas and the individuals length, which had a give initial value of 0.85 cm (based on observations, Fig. 2 on the supplementary material) in all mussel beds, ranges now from 2 to 3.5 cm. The other cohorts present the same pattern. Differences can even be observed within a mussel bed (Fig. 8), since a mussel bed is typically represented by a number of computational grid cells. The variability is high and within the same mussel bed it is possible that some of the mussels will spawn while others do not. The intensity of the spawning event can also differ, as it is shown for mussel bed M07. The comparison with observations is not very clear, due to the high variability and the sparse data, but it is possible to say that for most mussel beds, densities and biomass are in the same order of magnitude, although the biomass results seem to slightly deviate. Mussel beds contours estimations obtained by IMARES for spring 2009, reveals that most of the mussel beds existing in 2008 persist the year after, some of them with a slightly increase in area. Only a few, very small, new mussel beds were formed (Fig. 9). These results do not have a complete match with the results obtained in the SIBES program in 2009, regarding the presence of mussels in the collected samples. However, the surveys were done at different times, although in the same year. The model results obtained for June 2009 are generally consistent with IMARES contours, it also predicts the presence of new mussel beds but only a few are actually predicted at the same location as estimated by IMARES. In the model, some new mussel beds are formed in adjacent areas of existing mussel beds and some oth-

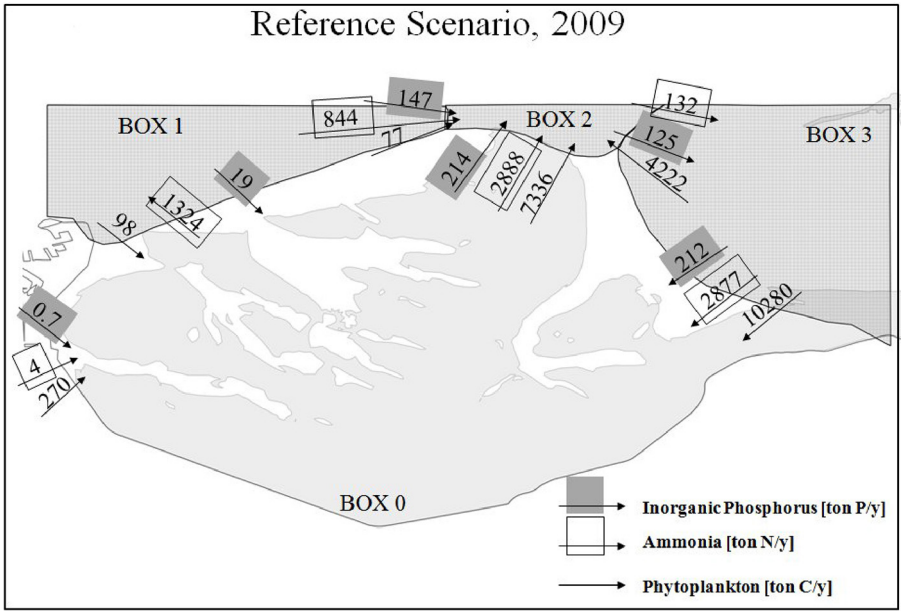

Fig. 6. Mass fluxes of properties between integration boxes, in the reference scenario, over 2009.

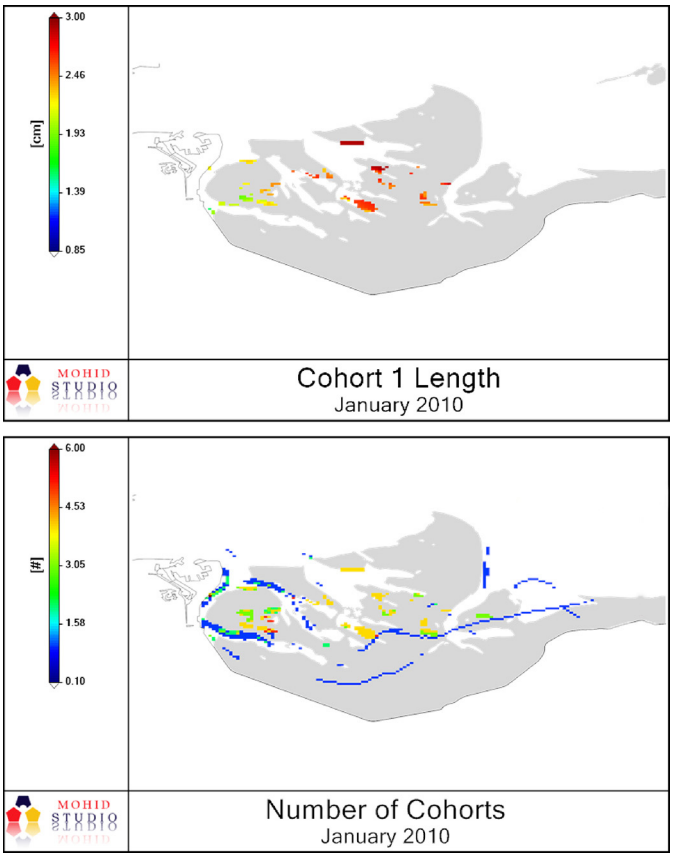

Fig. 7. Cohort 1 length and number of cohorts as predicted by the model for January 2010.

ers are located in and around the channels, where emersion times are high and velocity was not higher than 0.5 m/s.

Spatial variability within the same mussel bed is also apparent in the mussel reproduction buffer compartment and consequently in the timing, number and intensity of the spawning events. Spawning events are reflected in the number of cohorts (Fig. 10). The

Table 1
Relative importance (%) of each mortality process in the total loss of biomass (molC/m^2) per year, in mussel bed M05.

Mortality	2009	2010
Starvation	99.33	98.03
Natural	0.37	0.87
Settlement	0.049	1.0
Velocity	0.15	0.084
Cannibalism	0.0015	0.0067
Shrimps	0.0027	0.0003
Crabs	0.060	0.0044
Birds	0.042	0.0096

spawning season starts exactly when temperature rises above the threshold (9.6 °C), which in 2009, happened in the beginning of April, according to the model results. From that moment on, the spawning events are almost continuous during spring, summer and beginning of autumn, while the temperature is above the threshold. However, from all the new born cohorts (12 in 2009 and 15 in 2010), only a few (8 in 2009 and 3 in 2010) persist and in the beginning of the new year, most mussel beds have the same (or lower) number of cohorts as in the initial condition. Only a few areas, adjacent to existing mussel beds, have more than four cohorts. In fact, most cohorts die in their first month of life. Starvation is the main cause of biomass loss in an overall analysis (Table 1 and Fig. 11). It is responsible for more than 98% loss of the bivalve biomass, while total predation is only responsible for about 0.1% of the total biomass loss in 2009 and 0.02% in 2010. However, cannibalism has an extreme influence in the new born cohort density because it represents very high values of instantaneous mortality rate in the population (reaching a value of 10^5), which results in an strong decline in the cohort density and ultimately death of a new cohort (Fig. 12).

3.4. Bivalve's effect on ecosystem dynamics

In order to estimate the total influence of the mussel beds over biogeochemical processes in the Balgzand, model results were compared with a scenario without mussel beds (Fig. 13). In general, phytoplankton concentration is lower in the presence of bivalves as a result of mussel filtration, and nutrients concentrations are

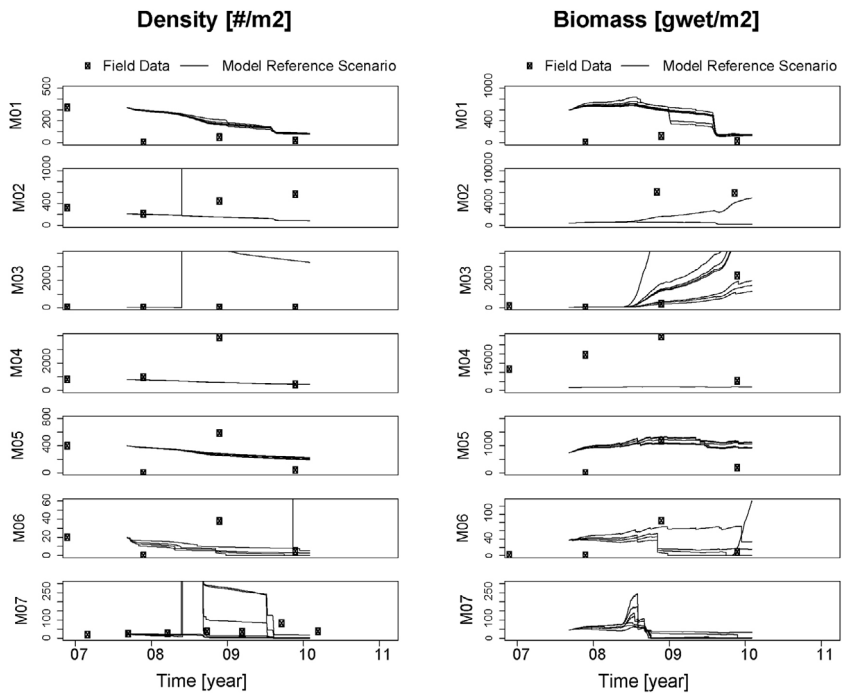

Fig. 8. Model vs. observations: density and biomass in the monitored mussel beds. Different lines represent model results in different cell of the domain that belong to the mussel bed.

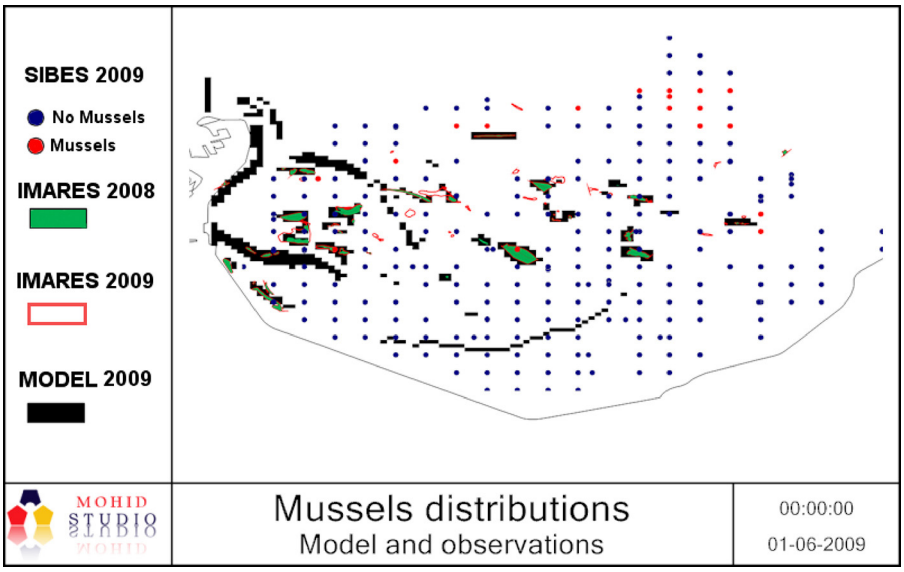

Fig. 9. Mussel bed distribution in spring 2009: model results obtained for June 2009; SIBES data obtained for 2009 and IMARES contour data estimated for spring 2009. IMARES 2008 correspond to the imposed initial distribution of mussel beds.

higher, due to mussels' excretions as well as an increase in the particulate organic matter mineralization. In a hypothetical scenario without mussels, the output flux of phytoplankton over one year would be about 15% more than the input flux, implying that the Balgzand is an area of intense primary production, that even exports biomass, certainly by consuming nutrients (Fig. 14). A net consumption of phosphorus is present in both scenarios, although more intense in the scenario without mussels. However, in the case of ammonia, model results indicate an export in both scenarios. This result suggests that the recycling of ammonia, by mineralization of organic matter is an important process in the system. Ammonia regeneration is responsible to fuel primary production and even to export about 40% more that the input flux.

4. Discussion

4.1. Physics

The Balgzand model setup was based on a downscaling approach using sub-model nesting. A larger area (Marsdiep domain) was simulated with a coarse resolution. The boundaries were located where data was available, in order to produce reliable and more detailed boundary conditions to a fine resolution sub-model, focusing only on the Balgzand (Balgzand domain). The underlying assumption is that the sub-model is influenced by the father model but, the sub-model does not affect the father model. The use of sub-model nesting was a viable option because: (a)

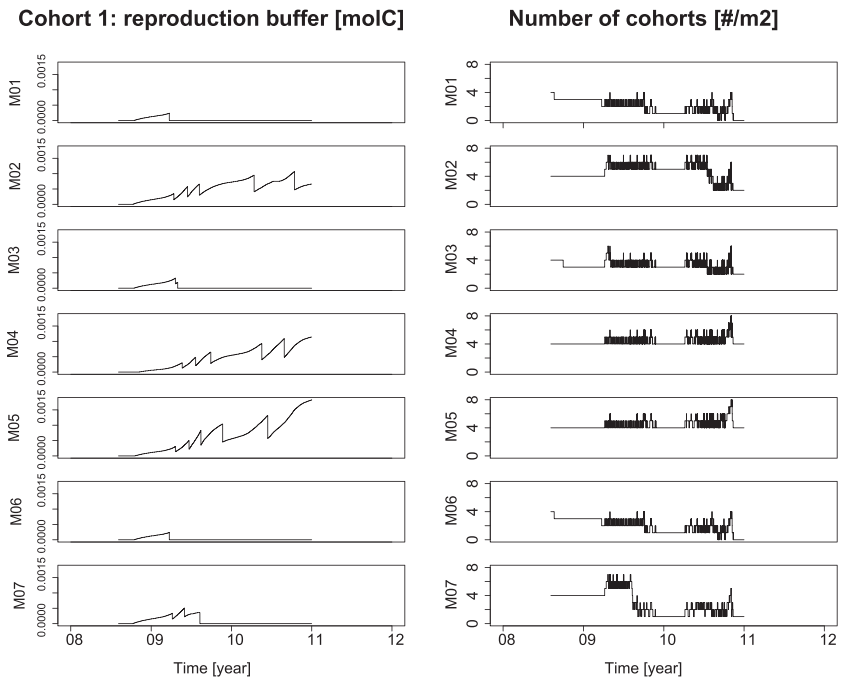

Fig. 10. Reproduction buffer and number of cohorts dynamics over time, in the monitored mussel beds.

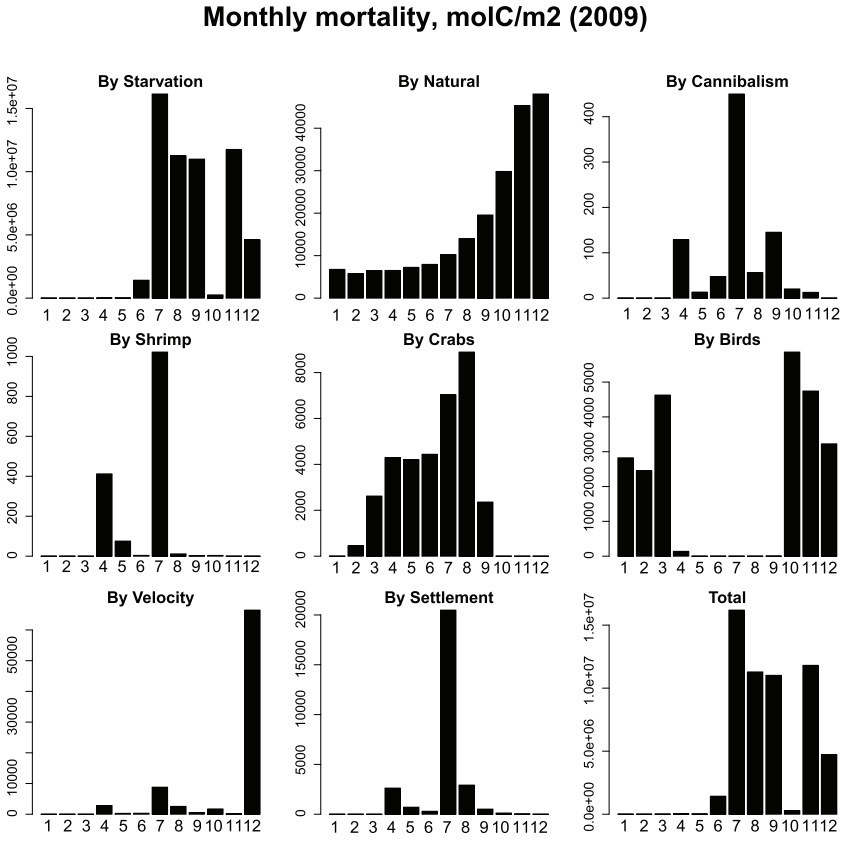

Fig. 11. Biomass loss by mortality process in the population, by month, during 2009, in mussel bed M05.

Balgzand presents particular environmental conditions as a consequence of its complex morphology and that it does not affect significantly other areas of the Wadden Sea; (b) comparisons at station 08, using the Marsdiep model and the Balgzand model confirms that the resolution of the model can be important to capture the high variability of the properties (Fig. 5). The use of a sub-model was thus, a good approach to increase the spatial resolution of the Balgzand domain, enabling a better discretization of the narrow channels and intertidal areas, without increasing too much the computational time. It is important to notice that this setup benefited from previous modelling studies, at the scale of the Wadden Sea and the North Sea (Duran-Matute et al., 2014; Philippart and

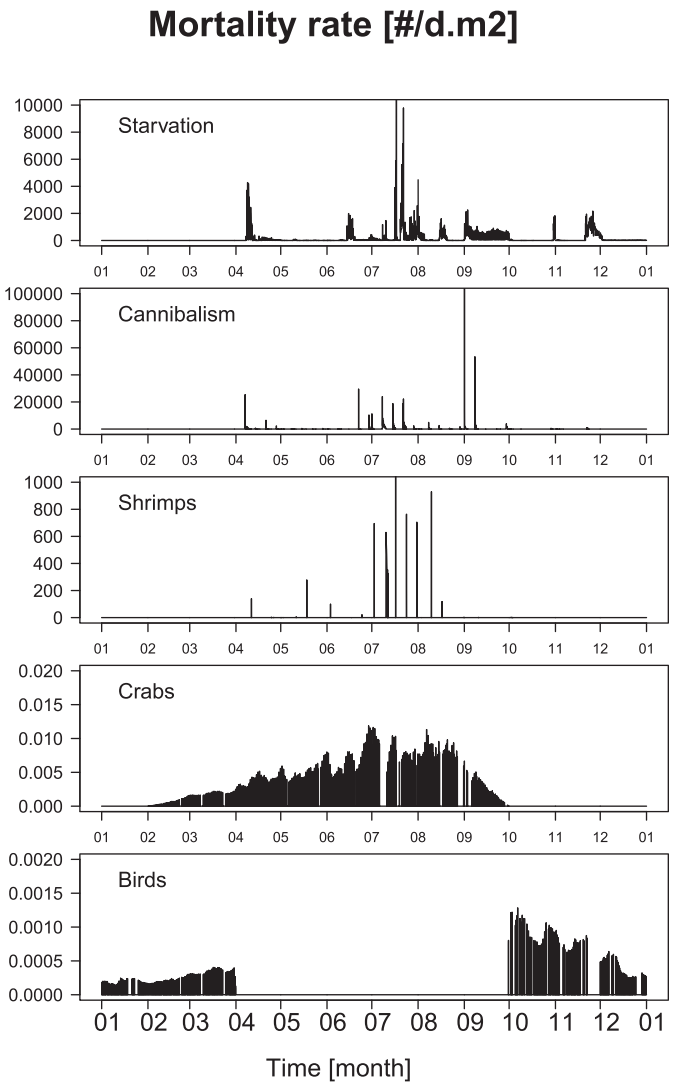

Fig. 12. Starvation, cannibalism, shrimps, crabs and birds instantaneously mortality rate in the population (sum of all the cohorts) during 2009, in mussel bed M05.

Hendriks, 2005), that provided high quality boundary conditions for the Marsdiep model.

Hydrodynamic results are only briefly presented, since that was not the main focus of this study. Validation is not detailed but the agreement between model results and field observations, on water level and temperature, suggests that the current velocities and overall transport is well simulated. The differences found in salinity and TSM concentrations are a result of the simplifications made for this particular setup, namely the use of a depth integrated approach. The sediment transport model, directly linked with particulate matter dynamics, used a simplified version of the processes. It considers only one type of fine sediments and parameters such as settling velocity (1×10^{-4} ms^{-1}), critical shear stress for erosion (0.75 Nm^{-2}), to deposition (0.3 Nm^{-2}) and the reference erosion rate (5×10^{-5} kg m^{-2} s^{-1}) were estimated by model calibration (results not shown). Tests were made within a range of values found in literature, and maintained constant for all simulations. Initial conditions for water column sediment concentrations and fine sediment distribution deposited in the bottom, were estimated also by the model. Starting from a homogeneous distribution, sediment transport dynamics was simulated for several months, until a more realistic depiction of the sediments spatial variability was achieved, by identifying erosion and deposition areas. These results were then used to feed the full model simulations as initial conditions. Bottom shear stresses control a great deal of the erosion and deposition processes and in shallow areas such as the Balgzand, wind waves, on top of currents, play an important role. The used wave model is based on wind velocity, direction and fetch. Although with limitations and despite being used in the Marsdiep domain where a part of the North Sea is simulated, it was deemed appropriate to simulate an area like the Balgzand. Wave results in the North Sea area of the Marsdiep model domain have to be considered with caution, as waves in this area are a product of regional propagation and local generation. However, results of simple model sensitivity analysis (not shown in this study) enable to conclude that variations on the wave parametrization were not relevant for wave and sediment transport dynamics in the Balgzand, as in addition to being a very shallow area, the Balgzand is shadowed from waves propagating from the North Sea. The wave model has additional restrictions in wind fetch calculations as it does not consider the effect of intertidal areas. Nevertheless, the assumptions are considered valid in line with the aim of the study and the results are in agreement with the observations.

4.2. Biogeochemical

In general, the Balgzand is an autotrophic and exporting system, i.e. there is biomass net production. Due to its shallowness, temperature, one of the main driving forces for biological processes, is extremely dependent on the heat balance with the atmosphere. In spring and summer, temperature is usually higher in the Balgzand compared to the Marsdiep domain, which triggers the extension of biogeochemical processes. As a result, phytoplankton and nutrients concentrations are also higher. Phytoplankton is high because primary production is intensified by temperature and light. Nutrients concentrations are higher, despite the high uptake by primary producers, because mineralization of organic matter and regeneration of nutrients due to bivalve's activity is also intensified. Although this study uses the simplest version of the pelagic biogeochemical processes model, the results proved that the model is able to capture the main seasonal patterns observed in terms of phytoplankton and nutrients. Phytoplankton concentrations are very well reproduced in the two field data stations, but nutrients seem to be systematically higher in the model, although in the same order of magnitude. This suggests that primary production is well simulated and that the differences found in the nutrient concentrations can be a result of the parametrization used for the mineralization of organic matter in the water column and/or in the sediment. In addition, the assumption of constant biomass composition can have an effect on the availability of the nutrients in the water column. Differences are more important in inorganic phosphorus concentrations in station 08, in the Balgzand. This station is located in a channel, close to the Oostoever discharge and as a result it is very influenced by the conditions imposed by this discharge. Because no specific information was found for both Helsdeur and Oostoever discharges, data from the Den Oever discharge was assumed (except for flow, temperature and salinity), which is possibly not very precise. This can be the main reason why concentrations on inorganic phosphorus are much lower than the observations.

4.3. Mussels

Mussels have an important effect in overall biogeochemical dynamics in the Balgzand. They globally intensify seasonal patterns, particularly in areas close to the mussel beds. This effect was quantified by comparing the reference scenario with a scenario without mussels. Phytoplankton concentration is lower in the presence of mussels, as a result of mussels' filtration, and nutrients concentrations are higher, due to bivalves' excretions, as well as an increase in

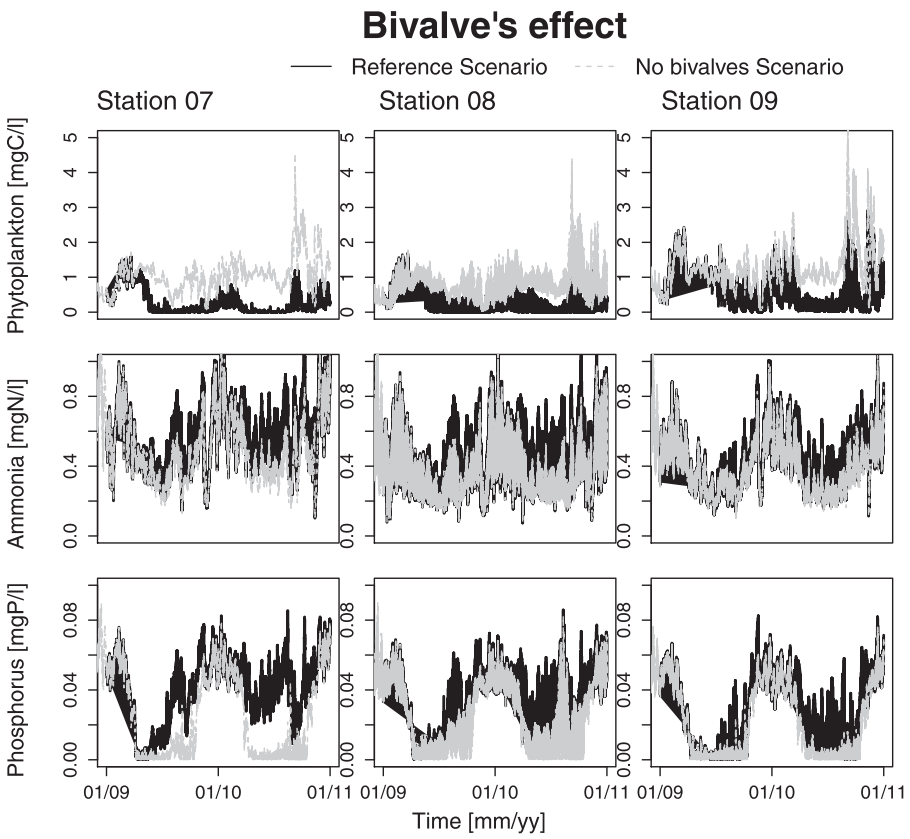

Fig. 13. Bivalve's effect on phytoplankton, ammonia and inorganic phosphorus dynamics, in stations 07 (mussel bed), 08 (Balgzand) and 09 (Amsteldiep).

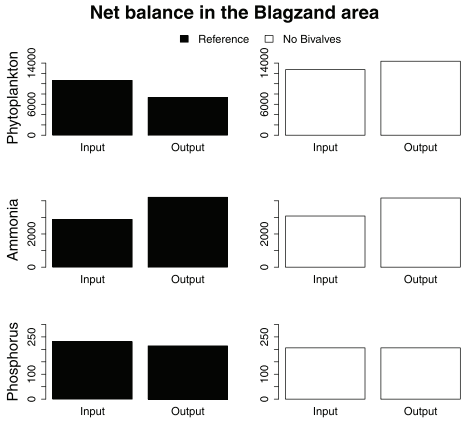

Fig. 14. Net balance of phytoplankton, ammonia and inorganic phosphorus in the Balgzand: reference scenario and scenario without bivalves.

the particulate organic matter mineralization. Nevertheless, mussels' density in the Balgzand mussel beds is not very high and their effect is mainly local, thus the overall spatial distribution of constituents is not greatly altered.

The model results indicate that the mussel spawning season in the Balgzand is long. The first spawning event starts when the temperature rises above the threshold imposed in the model, which in 2009 happens in early spring. Because the variability of the environmental conditions inside the system is relatively high, the individuals in each mussel bed have very different conditions, meaning that their reproduction buffer content is also variable. For that reason, spawning events are almost continuous in the period when the temperature is above the threshold, which has an interannual variability but can last about 6 months. After spawning, mussel larvae take, in the model, about 2–3 weeks to reach the settlement size (0.026 cm), which is in agreement with field observations (e.g. de Vooys, 1999). Dispersion is quite important and larvae are transported through the entire domain. This would suggest that open boundaries should be extended until the maximum area of dispersion. However, that would also imply the imposition of a larvae concentration at the open boundary, and observations are not available. For that reason and because the aim of the study is to focus only on the Balgzand area and to understand mussel beds dynamics in this area, a compromise solution was designed. Because larvae concentration at the open boundary is not known, it is initially considered to be null, meaning that only larvae generated inside the Balgzand domain are accounted for, and no external larvae are computed. When water exits the domain during ebb, it transports the larvae concentration calculated near the open boundary, but when it enters back it should not bring a null value of larvae concentration, as some of the water coming back in is in fact the same water that has left in first place. Thus, a time decay open boundary condition was used. This method computes the open boundary condition based on a reference value (null concentration) and on inner boundary concentration over a time scale. In this study a value of 3 h was used, which roughly accounts for half of a tide phase (ebb/flood), meaning the open boundary condition depends on the larvae concentrations values calculated at the boundary over the previous 3 h of simulation. This minimizes the effect of placing the open boundary where larvae concentrations are still high and avoids extending the domain boundaries, increasing computational efforts. This methodology also guarantees that larvae generated inside the domain will leave when crossing the open boundary but return to the Balgzand, depending on currents and fluxes at the boundary, but with a slightly lower concentration, that mimics the dilution/mixing outside the domain.

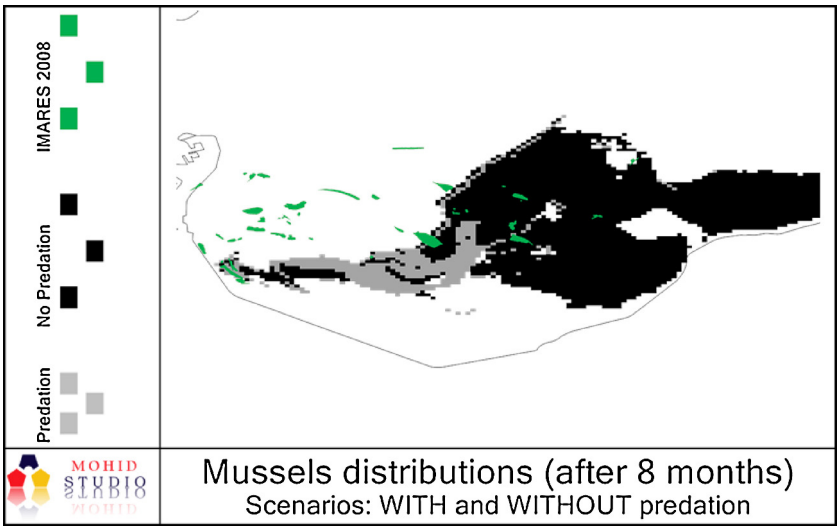

Fig. 15. Mussel distribution obtained with and without predators.

4.4. Predation

Larvae are subject to transport but also to cannibalism by adult mussels when they transit through a mussel bed and to starvation, to some extent. Cannibalism is, in fact, according to the model, a very important process. Although it is only responsible for less than 0.01% loss in the initial biomass, its instantaneous mortality rate in number of mussels can be very high and it happens during a very important life stage. The effects on the population dynamics are quite significant. For the two simulated years, most new cohorts die within the first month. When a new cohort does survive cannibalism, it still has to cope with the intense shrimp predation that occurs after reaching the shrimp minimum predation size. The start of shrimp predation coincides with the settlement, meaning that individuals are not transported any more and thus easily predated. In this way, the intense effect of cannibalism associated with the shrimps predation, can result in the extinction of most new cohorts in the existing mussel beds and the tendency is that new mussel beds are formed. The cohorts that were able to persist, were generated either in the beginning of the spawning season (early spring) or in the end (autumn), when the abundance of shrimps is not very high. Thus, the mortality processes at the beginning of their life cycle have an extreme importance and they can control the population dynamics at a particular location even if it does not represent the main mortality cause in an overall analysis. Starvation is the main cause of loss in terms of biomass and predation, either by adult bivalves or by other predators (shrimps, crabs and birds) is responsible for only about 0.1% of the total biomass loss. However, starvation is not responsible (in the reference scenario) for the death of a whole cohort and consequently not directly responsible for the cohorts' extinction, only for the reduction of their density. It is important to notice that the uptake by predators and their abundance is imposed in the model as a forcing function meaning that there is no direct feedback, only indirectly considered by the input data, which is monthly. This is a valid assumption for birds and even for crabs, but it is possible that this time scale its too high for shrimps because they growth faster and imposing monthly values will perhaps hide possible feedbacks. This can be a model limitation if in the future one aims to simulate or predict the variability of prey–predators dynamics dependent on environmental changes. Future developments and improvements can be implemented in the model regarding this topic.

Results from the two additional short scenarios: (1) with predators (shrimps, crabs and birds) and (2) without predators are shown in Fig. 15. The non predators area represents an optimal area for the mussels to establish based only on food availability. The presence of predators reduced the optimal area, meaning that they can also influence the spatial distribution of the mussel beds.

Results on bivalves do not deviate from the observations but it was also not possible to exactly quantify agreement with measurements. The distribution of mussel beds can be controlled by predation but it is, in the model, primarily controlled by the settlement probability, which was assumed as dependent on the amount of shells in the bottom. Therefore, most of the new mussel beds are formed in adjacent areas of existing mussel beds or former mussel beds. To avoid a complete restriction of mussel bed establishment, a minimum value of 0.1 was used for this parameter, and that explains why some of the new cohorts settled far from existing mussel beds, next or inside some of the channels. The channels, that in the Balgzand are not very deep would be, theoretically, perfect spots for new mussel beds because the intense water flow would guarantee food availability. However, strong velocities are also responsible for the detachment of individuals, and those will eventually die. This mortality process is responsible for designing the pattern of the 'mussel bed lines' (Fig. 7) that is not observed. New parametrization could be tested in order to obtain a pattern more consistent with the observations but perhaps a more realistic approach would be to use bottom shear stress to limit the individuals' settlement, rather than velocity. In this way the effect of waves and short storm events would also be taken into account.

An attempt at validating model results regarding mussel distribution, density and biomass was made using some of the existing data. In terms of spatial distribution, the comparison with the contours estimated by IMARES for the spring 2009 indicates the presence of some small new mussel beds and only a few are actually predicted by the model. But only a few are also detected in the SIBES program, probably because the aim of the monitoring programs is different and/or the sampling timing and methodology is also different. Model results indicate, as well as the observations, that most of the initial mussel beds persist and some of them increase in terms of area. It is important to notice that spring 2009 is only a few months after the start of the simulation and although the spawning season has already started, the mussel model properties are still very dependent on the initial conditions. More realistic results could perhaps be found using a longer bivalve model spin-

up and longer runs, but this was not possible yet as more input data would be needed. The comparison in terms of densities, in the monitored mussel beds is also difficult to interpret, because field data is sparse and there is high variability between different cells within the same mussel bed. However, the model and the observed densities are, for most mussel beds, in the same order of magnitude, which is considered to be in agreement at this stage. Observations in terms of biomass are always more challenging to predict because they depend on a higher number of factors. Additionally, the initial condition for bivalves, in this setup, was established based on their densities and length, and the correspondent biomass was not consistent with the measurements. This issue can also be subject of improvements in future implementations.

Finally, it is important to notice that the current study does not take into account other macrofauna existing in the system. New configurations of the model including other important species in the area (e.g. cockles) can be performed. The model is prepared for that and the only limitation would be the availability of data.

5. Conclusions

The process oriented modelling tool that results from the coupling between an individual-based population model for bivalves (based on the Dynamic Energy Budgets theory, DEB) and a hydrodynamic and biogeochemical model (MOHID Water Modelling System) was tested, for the first time, in a real system – The Balgzand (Wadden Sea, The Netherlands). The model proved to be able to respond properly to the environmental conditions dynamics and it is in agreement with the observations, particularly regarding hydrodynamics and water properties distribution (temperature, phytoplankton, nutrients). The analysis of the reference scenario results concludes that early stage mortality (top-down) can control the persistence of the new cohorts, in particular cannibalism and shrimp predation, although starvation (bottom-up) is the main process responsible for bivalve loss over the year in terms of biomass. It strengths that there is no single mortality factor responsible for the population dynamics regulation. The validation on mussel bed properties is hampered by the detailed model results that need to be synthesized and summarized to be comparable with the observations, which are usually sparse. The current study used many data sources from previous projects, studies and entities. A validation attempt was made and possible explanations for the deviations were identified. To illustrate its applicability, his study uses a scenario considering the nonexistence of mussel beds in the Balgzand to test and quantify their effect over local biogeochemical processes. More scenarios could be performed in the future, different parametrization could be tested and longer simulations could be performed to provide insight in the relative importance of a process. As an example, it could be interesting to test the influence of oysters and cockles on mussel growth; test the influence of temperature in prey–predators relations between mussels and shrimps; estimate possible locations for artificial mussel beds or characterize ecosystem response to different environmental scenarios. To our knowledge, this was the first integrated modelling study that focuses on mussel beds in the Balgzand.

The presented model can already be used to perform a wide range of studies concerning the effect of bivalves in the biogeochemical processes, as to estimate the impact of changes in the estuary morphology, location, existence or number of mussel beds (by natural or anthropogenic causes) on the ecosystem dynamics. The effect of changing environmental conditions in the bivalve population it self can be assessed by using the model in different scenarios and compare differences. The validation of the model at the mussel bed level still needs some attention but since the main processes are included and the dynamics of the properties are consistent with observations, differences between scenarios can be used to estimate effects and impact changes. Climate change studies can also be performed by using projected conditions for boundary and forcing conditions. In terms of development, at this stage, the model validation at the mussel bed level should be the main focus of future studies and it would be improved if more consistency between the different types of data is guaranteed. This can be archived, for instance, by sampling one mussel bed in detail, instead of several mussel beds. Information to be collected could include: water column properties measurements (including larvae concentration); abiotic properties; mussel bed extension and size distributions within the mussel bed; and individual mussels measurements (length and biomass), for a period of at least one year with variable sampling times depending on the season.

The complexity of the presented model is already high, but it is not yet limiting its implementation in real systems. In fact, the study suggests that some of the features could be improved by including a more detailed description of some of the processes. It is also important to mention that the model aims to be generic, meaning that it can be easily implemented in different systems, considering different bivalve species and even for more than one species. The first step was taken, but only more tests, implementations and improvements will give the model, and the scientific community using it, the desired experience to serve as an effective and reliable management tool.

Acknowledgements

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Appendix A. Residence time of the water in the Balgzand

Residence time of water in the Balgzand area was determined following the methodology proposed by Braunschweig et al. (2003),

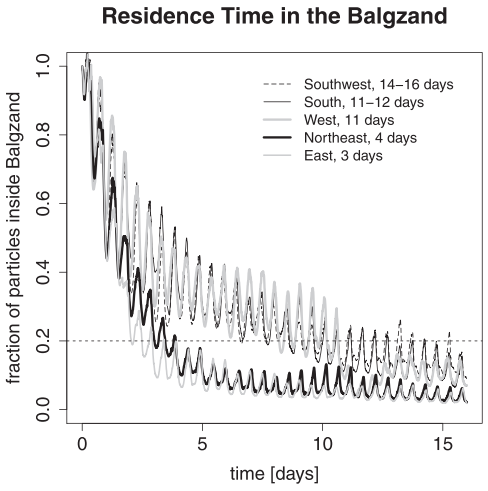

Fig. A.1. Balgzand residence time: fraction of lagrangian particles inside the Balgzand.

using a lagrangian approach. Residence time was computed by releasing an amount of lagrangian tracers, whose summed volume equals the water volume of the Balgzand area. The tracers are transported by currents and their position was tracked in relation to the Balgzand area. The fraction of tracers inside the Balgzand is calculated at each time step. Five scenarios were devised in order to understand residence time variability in relation with wind. The 2008–2010 wind data from De Kooy meteorological station were used. For each of the five most frequent wind directions, a period of 15 days was selected. The directions were selected based on frequency and importance in terms of hydrodynamic impact, e.g. East and Northeast wind induces stronger flushing of the water through the Marsdiep towards the North Sea, as Southwest and West winds will tend to block the water inside the Wadden Sea. Residence time was determined for each scenario by considering it as the time that approximately 80% of initial water volume had left the Balgzand area, and values ranged from 3 to 16 days (Fig. A.1).

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2017.04.018.

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